

Growth of *Dactylis glomerata* along a light gradient in the central Appalachian region of the eastern USA: I. Dry matter production and partitioning*

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Abstract

Microsite influences on resource allocation related to silvopastoral swards undergoing repeated defoliation are unclear. Defoliating traditional pasture species according to canopy development criteria may not be appropriate when the plants grow as understory crops in woodlots. An experiment using container-grown plants was conducted under field conditions to determine how open (O), shaded woodland (W) and open-to-shaded woodland transition zones (E_O , E_W), representing the partial shade conditions found in silvopastoral settings, influenced productivity and dry matter allocation in *Dactylis glomerata* L. Plants established in spring (SP) and late summer (LS) were clipped each time mean sward height reached 20 cm. Dry matter production differed for SP and LS plantings, and was greater in O than W sites. Dry matter allocation to shoots of SP plants indicated some agronomic benefit associated with the E_O and E_W sites. Leaf mass did not vary with irradiance, but stembase mass did. The SP plants had numerous small tillers whereas LS plants were composed of comparatively fewer but more massive tillers. Plants growing at O, E_O and E_W were similar, whereas plants in the W site were smaller and had the fewest tillers regardless of planting time. Results suggest that defoliation management for shaded components of silvopastoral systems should be based on some index other than sward height, and that management criteria might change during the growing season. Less intensive removal (e.g., 10-cm rather than 5-cm residue) should be considered for defoliated, shade grown plants, since this could allow more stembase and nonstructural carbohydrate storage tissues to remain.

Introduction

Microsites associated with complex topography and diverse plant communities in hilly terrain influence spatial and temporal boundaries of forage production. Land-use efficiency benefits when the mosaic of pasture and woodland, typical of hill-land regions, is used for silvopasture with

forages produced amongst trees for grazing livestock. Devkota and Kemp (1999) reviewed economic and ecological features of silvopasture in temperate regions and found that successful and productive systems depended on shade tolerant forages. Some forages, such as orchardgrass (*Dactylis glomerata* L.), common in pasture in the central Appalachian region of the eastern USA, are adapted to shade in temperate climates (Devkota et al. 1998; Lin et al. 1999). However, potential interactions among trees, understory

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swards, soils and grazers, complicate management decisions and may require reconfiguration of traditional practices to achieve acceptable herbage production and distribution.

Feldhake (2001) suggested that temperature and water conditions favored productivity of plants in shaded compared to open sites; however, no forage mass measurements were made. Woody plants facilitated grass productivity in warm regions, but suppressed co-occurring grass in cooler areas when moisture was adequate (Wilson 1998). Orchardgrass was productive under partial shade conditions when grown in alleys of coniferous tree plantations in the humid southeastern USA (Burner 2003).

Many grass species adjust to shade by increasing leaf length and specific leaf area to increase light acquisition, while at the same time slowing tiller production or vegetative propagation (Monaco and Briske 2000), compromising sward persistence. Defoliation (clipping or grazing) disrupts the light acquisition process. Forage productivity and persistence under low irradiance depend on post-defoliation leaf area, readily available non-structural carbohydrates, expression of new leaves and tillers, and regrowth of defoliated leaves to capture light and occupy sites in the sward.

Managing plant canopies based on development integrates morphological and phenological attributes with management and environment, and generally optimizes leaf production, which sustains herbage productivity (Parsons et al. 1988) and nutritive value. Defoliating cool-temperate forages as a function of sward height optimizes grazing livestock performance and sward persistence (Hodgson 1990), whereas decisions based on temporal criteria often ignore the integrative effect of plant development and environment. Relatively long intervals between defoliation events enable plants to generate leaf area and accumulate non-structural carbohydrates. However, this could lead to self-shading, resulting in fewer tillers and less shoot mass (Kays and Harper 1974) with leaf senescence exceeding leaf appearance (Parsons et al. 1988) and an overall decline in sward productivity and persistence.

Plant growth patterns and associated functions differ with size and occur at different rates as a function of size (Farrar and Gunn 1998). For comparative purposes, some adjustment for plant size or scaling is needed to provide an unbiased

means to assess DM allocation patterns. Since shade influences plant size, some commensurate change in allocation should take place (see Müller et al. 2000). Understanding allocation within the plant could help identify and design management practices that optimize leaf production and nutrient management in practical agricultural applications.

While benefits to grass productivity and persistence may accrue from microsite conditions associated with trees (Burner and Belesky 2004), precise management criteria for silvopastoral swards are unknown. Experiments were conducted to determine how conditions occurring in open pasture, heavily shaded woodland and pasture-woodland transition zones influenced productivity and dry matter allocation in orchardgrass, based on open pasture defoliation criteria. Woodland-pasture edges emulate the open shade conditions of silvopastoral systems. Light quantity was used as an index of site conditions, bearing in mind that it is associated with changes in light quantity and spectral composition, canopy and soil temperature, wind speed and water use by the sward (Morecroft et al. 1998). Productivity and allocation data are presented here, with details of growth mechanisms and nutritive value presented in companion papers.

Materials and methods

Plant culture

Orchardgrass, cultivar Benchmark, (early flowering) was sown (100 seeds pot⁻¹) in 2.5-L plastic pots containing a mixture of four parts soil (Lily, fine-loamy, siliceous, semi-active, mesic, Typic Hapludult) and three parts sand. Container-grown plants were used to minimize site and soil related effects on germination and nutrient availability (Monaco and Briske 2000). Dolomitic limestone (2 metric tons ha⁻¹) and hydrated lime (1 metric ton ha⁻¹) were applied to raise soil pH to 6.3 and added along with 35 kg ha⁻¹ N, P and K as commercial fertilizer (Peters Professional® All Purpose 20-20-20 from W. R. Grace & Co., Fogelsville, Pennsylvania, USA). Lime and fertilizer application was based on chemical analysis of soil.

Plants were grown for six weeks in a glasshouse, with a 14 h photoperiod, 24/18 °C light/dark

temperature and 55% relative humidity. Pots were placed outside in a non-shaded area for 2 weeks prior to placement at microsites in early May (spring planting, SP) or mid-August (late summer planting, LS) of 2001. The bottoms were removed from each pot at planting and pots were placed firmly in the ground to ensure uniform contact with soil. Microsites (81° 7' W; 37° 45' N; 850 m elev.) included an open (O) unobstructed pasture, a wooded (W) site dominated by *Quercus* spp. with 89.8% light attenuation relative to O, and two south-facing, edge (E) zones E_O and E_W with a growth interval mean of 30 and 56.4% light attenuation from similar tree species in W, respectively. The W and O sites were about 60 m apart and the transition sites midway between. Plants were fertilized with an annual split application totaling 100, 60 and 120 kg ha⁻¹ N, P and K with one-third of the total applied in May, early July and mid August in each year. Plants were watered (500 mL per pot) when precipitation was minimal during the growing season.

Microclimate conditions

Automated weather stations were installed at each site. Data collected at 2 m above the soil surface included light by radiometric quantum (LI-190SZ, LiCor, Lincoln, Nebraska, USA) and pyranometric (CM3 Pyranometer Kipp & Zonen B.V., Delft, Netherlands) sensors, maximum and minimum air temperature, precipitation, wind speed and relative humidity. Soil temperature was determined at soil surface and 5 cm depth. Values for ET_O (mm) were calculated according to the Penman–Monteith equation (Monteith and Unsworth 1990) based on air temperature, solar radiation, wind speed, relative humidity, longitude, latitude and elevation above sea level.

Sample collection and analysis

Baseline data were collected from nine replicates immediately prior to planting time, at which time all plants were clipped to a 5-cm residual plant height. Three replicates (initial total of 24 replicates at each site), were collected and a destructive sampling made each time mean plant height reached 20 cm. Plant height, tiller number, leaf (> 5 cm above soil surface), stembase, (soil surface to 5 cm)

and root mass were determined. Remaining plants were clipped to 5 cm and allowed to regrow to 20 cm. Tissues were lyophilized and mass determined. Plants (grasses and forbs) surrounding orchardgrass plants at each microsite were clipped to 5 cm height each time experimental plants were clipped.

Parameter calculations

All calculations are on a per tiller basis, with leaf data normalized for 15 cm of top growth. A linearized allometric regression equation was used to model DM allocation as a function of plant size (Shipley and Meziane 2002). The calculation used in this experiment included stembase as part of the leaf and assumed the form:

$$\ln(M) = a + b \ln(M)$$

where M_S = DM (g) of shoot (leaf + stembase) and M_R = DM (g) of root.

Stembase was included in the shoot component because new leaves originate and nonstructural carbohydrates are stored there in cool-temperate perennial grasses.

Statistical analysis

Cumulative leaf, shoot (leaf + stembase) and root yield data were analyzed using SAS-MIXED procedure. Leaf mass was the total of a series of harvests for an entire growth interval, whereas root and stembase mass was determined at the end of the entire interval. Light attenuation (sites O, E_O , E_W or W) and planting time were fixed effects and replication was random in the model. Years were separated in the model for analysis of light and planting time. Cumulative leaf, shoot and root mass data were modeled using SAS regression procedures to determine goodness-of-fit based on planting time.

Total DM, DM of leaf, stembase, root and shoot:root ratio were analyzed with SAS-MIXED procedures. Replication and interactions with replicate were random and light, harvest and planting time fixed effects. Denominator degrees of freedom were calculated using the Satterthwaite option, and were used for testing mean square estimates, standard errors and *t*-ratios for multiple error terms.

Table 1. Representative microclimate conditions for the 2001 and 2002 growing seasons in the central Appalachian region of the eastern USA.

	Open (O)		Edge open-woods (E_O and E_W)		Woods (W)	
	2001	2002	2001	2002	2001	2002
PPFD(mol m ⁻²) ^a	— ^b	5395	3248 (E_O); 1535 (E_W)		—	552
ET_O						
May	22.4	47.1	18.3	18.3	6.3	7.5
July	47.2	47.1	11.5	48.8	2.2	2.0
August	5.4	21.5	2.7	14.2	0.3	1.2
September	6.1	4.8	3.8	3.2	0.5	0.5
Precipitation (cm)						
May	7.65	4.91	—	3.95	—	3.80
June	3.18	2.53	—	1.57	—	1.81
July	9.65	5.33	—	4.14	—	5.26
August	2.38	0.98	—	0.57	—	0.64
September	1.35	2.91	—	1.92	—	2.24
October	0.71	4.78	—	3.58	—	3.83
November	0.66	4.90	—	3.90	—	3.91

^aLight data (PPFD) collected April 1 through October 31.

^bNo data were collected where (—) appears.

Results and discussion

Microsite conditions

Mean monthly precipitation, photosynthetic photon flux density (PPFD) and potential evapotranspiration (ET_O) are presented in Table 1, where microsite differences were consistent with trends reported by Morecroft et al. (1998) for deciduous woodland compared to open pasture. Light (cumulative) was used as a relative indicator of microsite differences for the respective growth intervals at any given microsite in 2002. Total PPFD ranged from 5395 mol m⁻² at O to 552 mol m⁻² at W sites. Predicted evapotranspiration (ET_O) was greatest at O and least for W and was much less in September than May for both SP and LS plantings. Daily mean air temperatures were similar among sites (data not shown), but daily mean soil temperatures (5 cm depth) were about 5 °C less at W than other sites. The young SP plants encountered increasing temperatures and daylength with the onset of summer, and probably increased competition for water and light in E_O , E_W and W. Comparably aged LS plants encountered decreasing temperature and daylength when placed at microsites, and less competition for light in shaded sites at certain times because of leaf fall and sun angle prior to winter

and cessation of growth. The LS plants received higher light amounts in early spring prior to leaf appearance on trees in E_O , E_W and W sites, but temperatures were not yet favorable for vigorous LS leaf growth.

Dry matter distribution

Leaf mass was similar for all plants at planting. The season-long proportion of leaf relative to whole-plant mass was not influenced by irradiance or planting time (Figure 1). However, differences associated with light attenuation did occur in roots and stembases, and agree with observations made by Poorter and van der Werf (1998) and models of mass distribution proposed by Müller et al. (2000). About 60% of total mass of SP plants was root, from 20 to 30% stembase and 10–15% leaf. Late-summer sown plants had more DM as root (75%), less as stembase (5–10% of total) and leaf similar (10–15%) to SP plants. Stembase mass may be related to the number of tillers.

Variation in tiller number and rate of tiller change was a function of the interaction of planting time and light regimen. Changes in the number of tillers for SP plants were large and showed an overall tiller loss, whereas LS plants had a much slower rate of tiller loss and tended to

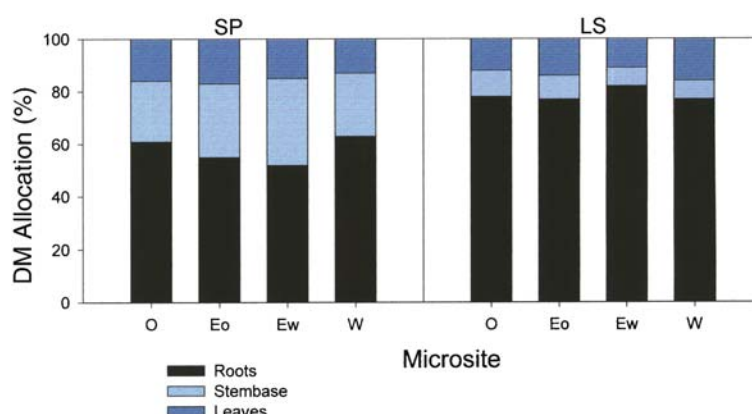


Figure 1. Dry matter allocation among leaves, stembases and roots of orchardgrass plants sown in spring (SP) or late summer (LS) in the central Appalachian region of the eastern USA. Values represent the mean of all harvests for respective microsites and planting times.

remain at a balanced (e.g., appearance balancing loss) population (Figure 2a). The SP plants at O recovered slightly in tiller appearance later in the growth interval, whereas plants at W continued to lose tillers with successive harvests (data not shown, but reflected in large s.e.m. for SP plants shown in Figure 2a).

Tiller number decreased as light attenuation increased, with plants grown in W with the fewest and O the most tillers compared to plants at other sites, irrespective of planting time (Figure 3). Shading and associated changes in light quality (i.e., red:far-red relationships) decrease tiller production in grasses (Deregibus et al. 1985). Planting time influenced tiller number with more tillers on SP than LS plants (Figure 3). The SP plants increased or occupied sites by producing more tillers, whereas LS plants could produce seed (vernalized plants) and tillers and generated fewer but relatively larger tillers. Dry matter tiller⁻¹ was high in LS plants and varied widely, whereas SP plants varied most in tiller number and less in terms of DM tiller⁻¹ as a function of light attenuation. Consequently, plants growing at W had the lowest DM tiller⁻¹ (LS) or the fewest tillers (SP) when compared to plants growing at other sites.

Shoot:root

Photosynthate allocation expressed as a simple mass fraction of shoot:root (S:R) differed between SP and LS plants (Figure 2b). The fraction reflects

DM distribution (see Figure 1) and suggests that as total plant mass increased, S:R decreased for SP plants. Shoot mass of SP plants was similar to that of LS plants, but maximum root mass of SP plants was only about 33% of that obtained by LS plants. Shoot:root decreased with successive harvests in SP (decrease of ~60% from the first to last harvest) and to a lesser degree (decline of ~30%) in LS plants (data not shown).

Differences in S:R between SP and LS plants could be a function of physiological capabilities of vernalized (LS) and non-vernalized (SP) plants (Troughton 1960), or microclimate conditions and nutrient acquisition characteristics. Older roots are much less involved in nutrient capture and, as plants age the relative proportion of younger, more active roots decreases. While the fraction presented gives us some appreciation of DM partitioning, it provides us with no understanding of photosynthate allocation associated with changing plant size and growth strategy. One means of understanding allocation irrespective of size is to apply allometric analysis to the data that reflects net fluxes of photosynthate.

Allometric S:R was < 1:1 when plants were SP-sown suggesting strong allocation to roots (Figure 4). Allometric S:R was ~1:1 for LS-sown plants, suggesting that plants were well-established and allocated similar amounts of photosynthate to shoot and root. Differences attributable to light attenuation in SP were slight and not detectable for LS plants. More photosynthate tended to be allocated to root in SP plants. The smaller SP

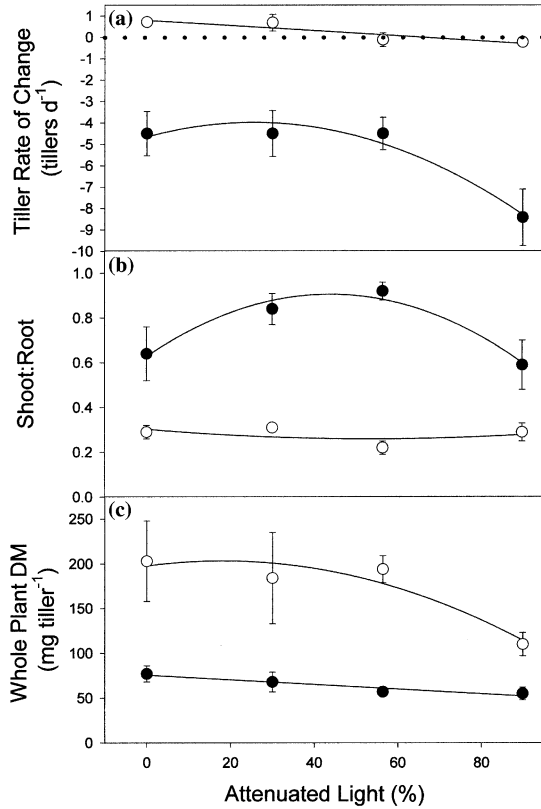


Figure 2. (a) Tiller rate of change (Tillers d^{-1}); (b) shoot:root; and (c) whole plant (shoot and root) dry matter (DM) as a function of light attenuation for orchardgrass plants established in spring (SP; closed symbol) and late-summer (LS; open symbol) in the central Appalachian region of the eastern USA. Regression equations; $\Delta T_{SP} = 5.31 \times 10^{-2} (x) - 1.04 \times 10^{-3} (x^2) - 4.66$, $r^2 = 0.96$; $\Delta T_{LS} = -1.21 \times 10^{-2} (x) + 7.91 \times 10^{-1}$, $r^2 = 0.83$. $S:R_{SP} = -1.27 \times 10^{-2} (x) - 1.45 \times 10^{-4} (x^2) + 6.28 \times 10^{-1}$, $r^2 = 0.96$; $S:R_{LS} = -1.61 \times 10^{-3} (x) + 1.49 \times 10^{-5} (x^2) + 3.03 \times 10^{-1}$, $r^2 = 0.86$. $DM_{SP} = -2.57 \times 10^{-1} (x) + 75.58$, $r^2 = 0.92$; $DM_{LS} = 6.22 \times 10^{-1} (x) - 1.73 \times 10^{-2} (x^2) + 197.74$, $r^2 = 0.89$.

plants fit the balanced growth model proposed by Shipley and Mezaine (2002) where allocation to roots exceeded that to shoots for very young plants. Allocation to shoots in LS compared to SP plants adheres to the allometric model proposed by Müller et al. (2000) and reflects the presence of relatively fewer but more massive tillers. Allometry data support the premise that development (e.g., young nonvernalized vs. older vernalized plants) influences allocation (Poorter and Nagel 2000).

Physiological efficiency does not supplant size related competition (e.g., big plants intercept more incoming light but may not have more efficient

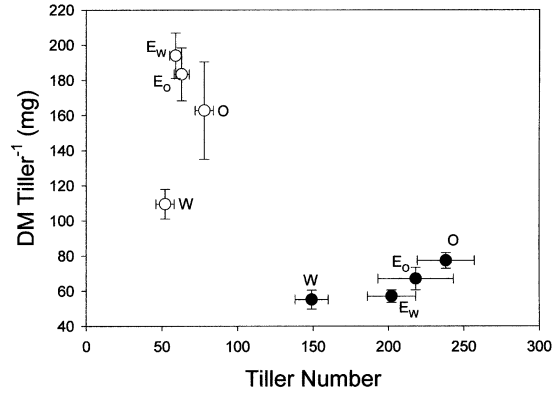


Figure 3. Dry matter mass per tiller expressed as a function of tiller number for plants established in spring (closed symbol) and late-summer (open symbol) growing in open (O), edge (E_o ; E_w) and wooded (W) sites in the central Appalachian region of the eastern USA.

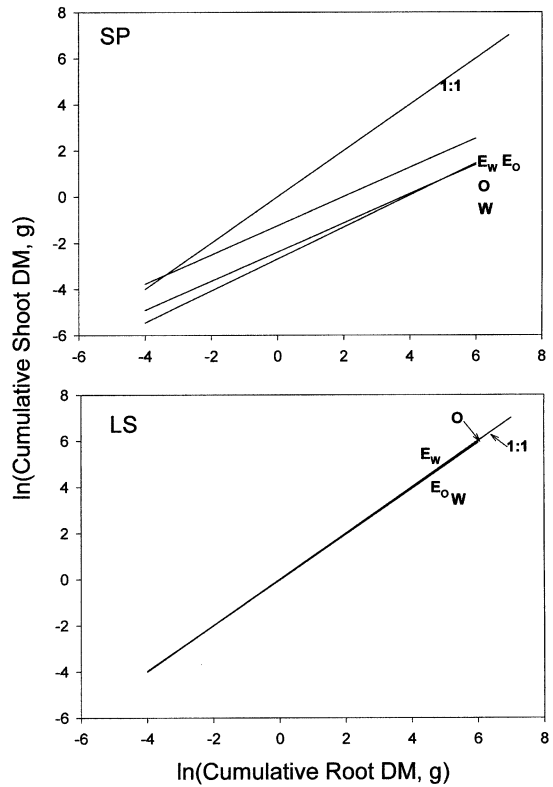


Figure 4. Allometric relationship of shoot and root mass of plants established in spring (SP) and late-summer (LS) growing in open (O), edge (E_o ; E_w) and wooded (W) sites in the central Appalachian region of the eastern USA. Allometric regressions shown in Table 2.

Table 2. Allometric regression equations computed according to Shipley and Meziane (2002) for shoot and root dry matter for spring (SP) and late-summer (LS) planted orchardgrass grown along a light gradient in the central Appalachian region of the eastern USA.

SP	
O ^a	$\ln(M_s) = -1.49 + 0.53 \ln(M_r) R^2 = 0.96 SE_{\text{est}} = 0.19$
E _O	$\ln(M_s) = -1.27 + 0.64 \ln(M_r) R^2 = 0.97 SE_{\text{est}} = 0.22$
E _W	$\ln(M_s) = -1.25 + 0.63 \ln(M_r) R^2 = 0.96 SE_{\text{est}} = 0.24$
W	$\ln(M_s) = -1.75 + 0.48 \ln(M_r) R^2 = 0.98 SE_{\text{est}} = 0.15$
LS	
O	$\ln(M_s) = 0 + 1.00 \ln(M_r) R^2 = 1.00 SE_{\text{est}} = 0.00$
E _O	$\ln(M_s) = -0.01 + 0.99 \ln(M_r) R^2 = 1.00 SE_{\text{est}} = 0.01$
E _W	$\ln(M_s) = 0.01 + 1.00 \ln(M_r) R^2 = 0.99 SE_{\text{est}} = 0.03$
W	$\ln(M_s) = -0.02 + 0.99 \ln(M_r) R^2 = 1.00 SE_{\text{est}} = 0.01$

^aMicrosites included open (O), edge (E_O or E_W) and wooded (W) sites. M_s = Dry mass of leaf + stembase (g), M_r = Dry mass of root (g).

photosynthetic metabolism). Apparently, larger or well-established plants represented by LS plants in this experiment are nominally influenced by changes in microsite conditions as shown by slopes and allometric coefficients of the regression lines (Table 2). Larger plants (in this case total mass) are likely to be more resilient and resistant to disturbance and from an agronomic perspective, persistent and productive components of swards. This assumes that allocation to a structure in repeatedly defoliated plants is proportional to function and reflects plant growth rate (Oosterheld and McNaughton 1991) (Table 3).

Cumulative dry matter production

Total whole plant DM was greater in LS than SP plants irrespective of light (Figure 2c). Dry matter production was proportional to light and varied less in SP than in LS plants. The relationship of DM and light was statistically significant but numerically small for SP plants. Results were similar to those obtained by Burner (2003) for orchardgrass growing in shaded compared to open environments in a similar physiographic region. Plant response to site conditions, depending on planting time, influenced duration of growth and ultimately number of harvests and cumulative total herbage production. Cumulative leaf and root DM of repeatedly defoliated plants differed with planting time, but shoot mass did not. Season-long trends are shown in Figure 5. The SP shoot mass

Table 3. Regression equations for leaf, shoot (leaf + stembase) and root cumulative dry matter for spring (SP) and late-summer (LS) planted orchardgrass growing along a light gradient in the central Appalachian region of the eastern USA.

Leaf	
SP	
O ^a	$y = 4.37 \times 10^{-1}(x) - 50.45 R^2 = 0.99$
E _O	$y = 4.71 \times 10^{-1}(x) - 56.29 R^2 = 0.94$
E _W	$y = 6.09 \times 10^{-1}(x) - 81.35 R^2 = 0.99$
W	$y = 3.40 \times 10^{-1}(x) - 40.18 R^2 = 0.95$
LS	
O	$y = 5.59 \times 10^{-1}(x) - 41.89 R^2 = 0.88$
E _O	$y = 6.81 \times 10^{-1}(x) - 60.13 R^2 = 0.87$
E _W	$y = 6.15 \times 10^{-1}(x) - 55.99 R^2 = 0.97$
W	$y = 6.27 \times 10^{-1}(x) - 58.31 R^2 = 0.96$
Shoot	
SP	
O	$y = 1.02(x) - 113.33 R^2 = 0.99$
E _O	$y = 1.06(x) - 115.77 R^2 = 0.94$
E _W	$y = 1.89(x) - 244.44 R^2 = 0.99$
W	$y = 0.86(x) - 91.63 R^2 = 0.95$
LS	
O	$y = 0.99(x) - 75.73 R^2 = 0.88$
E _O	$y = 1.06(x) - 89.44 R^2 = 0.87$
E _W	$y = 1.06(x) - 97.94 R^2 = 0.97$
W	$y = 0.91(x) - 80.62 R^2 = 0.96$
Root	
SP	
O	$y = 1.95(x) - 258.76 R^2 = 0.99$
E _O	$y = 1.44(x) - 171.92 R^2 = 0.98$
E _W	$y = 2.07(x) - 271.59 R^2 = 0.99$
W	$y = 1.79(x) - 224.84 R^2 = 0.99$
LS	
O	$y = 3.89(x) - 332.66 R^2 = 0.91$
E _O	$y = 3.78(x) - 330.00 R^2 = 0.86$
E _W	$y = 5.33(x) - 541.41 R^2 = 0.96$
W	$y = 3.45(x) - 323.92 R^2 = 0.97$

^aMicrosites include open (O), edge (E_O or E_W) and wooded (W) sites.

reflects the large number of small tillers and mass allocated to vegetative propagules in establishing plants (Figure 3). While leaf mass was greater in LS than SP, relative fractional proportion of total mass was similar (Figure 1). Root mass of LS was about twice that of SP plants and contributed to significantly greater total DM of LS compared to SP plants (Figure 2c).

The duration of sustained growth (time from placing plants at the microsites until the last harvest) varied with site. The defoliation schedule was determined by canopy development (leaf extension) and not just time. Although duration of growth varied, five harvests were made at each site

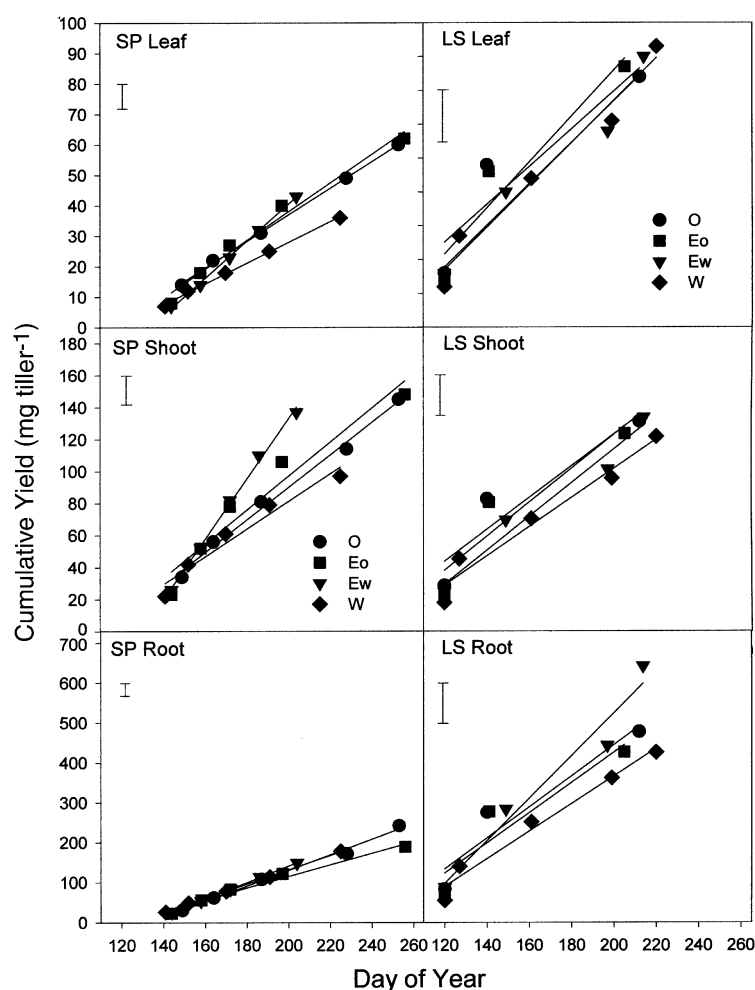


Figure 5. Cumulative yield of leaf, shoot (leaf + stembase) and root of orchardgrass sown in spring (SP) or late summer (LS) in the central Appalachian region of the eastern USA. Lines are linear regression models (regression equations shown in Table 3) for shoot and root dry matter.

for SP plants. The LS plants at O and E_O sites were harvested three times compared to four for E_W and five for W. In some instances during the LS growth interval, E_W and W plants were harvested when O and E_O plants were not (Figure 5). This pattern could provide herbage at times during the growing season when production from open pasture lags because of microclimate factors (see Table 1). The average canopy height index used to define a harvest was reached in W and E_W sites because leaf elongation was occurring as a response to shade. Harvesting shade-grown orchardgrass depends on defining an interval that allows for optimal re-growth of leaf while minimizing additional stress from the occurrence of self-shading.

Repeatedly defoliated orchardgrass had different growth and resource allocation patterns associated with planting time (SP, juvenile plants harvested in the same season in which they were planted; or LS, vernalized plants harvested in the season following establishment and a period of winter dormancy). More DM occurred as leaf in plants growing in transition zones (E_W and E_O) than in extremes of too much (O) or too little (W) light suggesting that partial shade is a means of facilitation. Root:shoot quotients and allometric data indicate that growth and allocation patterns of repeatedly defoliated LS plants were stable under the range of conditions imposed in this experiment, although microsite conditions

influenced plant size (e.g., fewer and smaller tillers as light attenuation increased). Plant attributes other than leaf mass (i.e., stembase mass and tiller number) of established plants reflect management and environmental conditions.

Forage-based livestock production systems depend on sustained leaf production to meet livestock nutritional requirements, but leaf production should not be achieved at the expense of structures contributing to plant persistence (Donaghy and Fulkerson 1997). Allocation reflects physiological and developmental state as a function of environment, expression of genetic potential and in the case of agronomic applications, management. Indices of resource use efficiency and nutritive value are presented in companion papers where morphological (e.g., specific leaf area, leaf mass ratio) and physiological (e.g., nonstructural carbohydrate characteristics; net assimilation rate) components of growth are considered (Belesky 2000-b; Belesky et al. unpublished data).

Typically, pastures are sown in spring in cool-temperate climates, but in areas where summer temperatures are high and moisture limited, late summer planting occurs. Productivity of SP plants varied whereas that of LS plants was stable under the range of light conditions imposed. A less intensive removal (e.g., 10-cm rather than 5-cm residue) of available herbage might allow more stembase tissue to remain and contribute to stand persistence (Fulkerson and Donaghy 2001). Defoliation based on a greater target canopy height or longer intervals between harvests could lead to self-shading and accelerate stand loss. Defoliation regimen could interact with plant response to microsite conditions linked to tree leaf appearance and loss, weather patterns, defoliation and nutrient inputs. Harvest frequency and intensity issues are unresolved for shade grown forage and warrant further investigation.

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